

## Spatial Scale of Fenvalerate Resistance in Pear *Psylla* (Homoptera: Psyllidae) and Its Relationship to Treatment History

BRUCE E. TABASHNIK, BRIAN A. CROFT,<sup>1</sup>  
AND JAY A. ROSENHEIM

Department of Entomology, University of Hawaii,  
Honolulu, Hawaii 96822

J. Econ. Entomol. 83(4): 1177-1183 (1990)

**ABSTRACT** Data on fenvalerate susceptibility, pyrethroid use, and related information for 48 sites in British Columbia, Washington, Oregon, and California were analyzed to clarify the spatial scale and causes of fenvalerate resistance in pear psylla, *Psylla pyricola* Foerster.  $LC_{50}$ 's for fenvalerate varied significantly among regions and subregions. The number of pyrethroid treatments per site explained a significant portion of the variation in fenvalerate  $LC_{50}$  over all sites, within regions, and within subregions. For a given number of pyrethroid treatments, the expected  $LC_{50}$  for fenvalerate varied significantly among regions and subregions. Within-season timing of pyrethroid treatments, continuity of pyrethroid use, intensity of pear production in the surrounding area, and number of pyrethroid treatments at neighboring sites were not significantly associated with  $LC_{50}$ 's for fenvalerate. Prospects for managing resistance to fenvalerate are best in Oregon and California (where levels of resistance were generally lower) compared with Washington and British Columbia. Results showing that local variation in  $LC_{50}$  for fenvalerate was significantly associated with local variation in pyrethroid use suggest that growers can reduce local increases in resistance by limiting pyrethroid treatments.

**KEY WORDS** Insecta, *Psylla pyricola*, resistance management, pyrethroids

PESTICIDE RESISTANCE is one of the most serious problems in agriculture (National Research Council 1986, Roush & Tabashnik in press). Resistance management, which seeks to slow or reverse evolution of resistance in pests, requires an understanding of the spatial scale of resistance and the factors that influence resistance development in field populations. If resistance is caused primarily by factors that operate locally, such as local variation in pesticide use, then management of resistance by individual growers may be possible. Alternatively, management of regional resistance requires regional cooperation (Miranowski & Carlson 1986). Although resistance has been documented in at least 447 species of insects and mites (Georghiou 1986), few rigorous attempts have been made to separate regional and local variation or to identify causes of geographical variation in resistance (Follett et al. 1985, Rosenheim & Hoy 1986, Tabashnik et al. 1987).

In principle, the best way to test hypotheses about the evolution of resistance is to conduct controlled, replicated field experiments. Practical constraints limit the feasibility of this approach, however. Of particular concern is the potential for field exper-

iments to exacerbate the resistance problem by generating new resistances in field populations of pests (Taylor 1983). Other drawbacks include the relatively long time that may be required (perhaps 1-10 yr) for field resistance experiments, the difficulty in isolating treatments spatially so that gene flow between treatments is negligible, and the expense and logistics of obtaining sufficient replication.

An alternative to field experiments is retrospective analysis of geographical variation in pesticide resistance in conjunction with information on pesticide use history and other potentially important factors (Tabashnik 1986). For example, Rosenheim & Hoy (1986) found that susceptibility to pesticides in *Aphytis melinus* Debach (Hymenoptera: Aphelinidae), a parasitoid of California red scale, was correlated with histories of pesticide use within groves and counties.

Our study was done to increase understanding of resistance development in pear psylla, *Psylla pyricola* Foerster, a major pest of pear in the western United States and Canada. Pear psylla typically evolves resistance in many areas of pear production within 5-10 yr after a new insecticide is introduced (Westgard & Zwick 1972, Riedl et al. 1981, Follett et al. 1985, Croft et al. 1989, van de Baan et al. 1989). The pyrethroid fenvalerate was first used to

<sup>1</sup> Department of Entomology, Oregon State University, Corvallis, Ore. 97331.

control *P. pyricola* in the United States in 1979 and in Canada in 1980; surveys of fenvalerate resistance were conducted from 1982 to 1988 (Croft et al. 1989).

We conducted a retrospective analysis of development of resistance to fenvalerate in *Psylla pyricola* at 48 sites in British Columbia, Washington, Oregon, and California. We used bioassay data and information on pesticide use and related factors (Croft et al. 1989) to compare regional variation (between state or province) with subregional variation (within state or province) in fenvalerate resistance, to determine the relationship between history of pyrethroid use (within orchards and subregionally) and fenvalerate resistance, and to assess the relationship between intensity of pear production and fenvalerate resistance.

### Materials and Methods

**Data Collection.** Bioassay data, histories of pesticide use, and related information were obtained from Croft et al. (1989), which describes methods in detail. Postdiapause pear psylla adults were collected in orchards from 27 January to 17 March 1988. A total of 150–600 field-collected psyllids in four replicates for each population were tested in laboratory slide-dip bioassays (Follett et al. 1985) with fenvalerate to estimate  $LC_{50}$ . Psyllids were anesthetized with carbon dioxide, mounted on sticky tape, dipped for 5 s in fenvalerate dilutions, held for 48 h at 23°C, and then checked for mortality. Histories of pesticide use at each site, including total years of pyrethroid (mostly fenvalerate) use, mean number of pyrethroid applications per year, timing of sprays (prebloom, summer, neither, or both), and continuity of annual pyrethroid use (continuous or noncontinuous), were based on a survey of the growers, consultants, or research personnel responsible for pest management at each site. Intensity of pear production in the area surrounding each site (low, medium, or high) also was estimated by the survey.

**Analysis.** Each state (Washington, Oregon, California) or province (British Columbia) was considered a region. Nine subregions were also defined by Croft et al. (1989): Washington and Oregon had three, California had two, and British Columbia had only one.  $LC_{50}$ 's for 48 sites were obtained from Croft et al. (1989); two sites with indeterminate  $LC_{50}$  values (Antelope, Oreg. and Carter, Calif.) were excluded from our analysis. Several "organic/low spray" sites were purposely included in the study by Croft et al. (1989) (two in British Columbia, four in Washington, one in Oregon, and one in California). If these sites were not representative of their subregion or region, then their inclusion in our analyses could have biased some of our conclusions. To address this problem, analyses that might have been biased by this effect were done with and without the organic/low spray sites. In all but two cases, conclusions were virtually iden-

tical with and without these sites, and results are reported with the organic/low spray sites included. In the two exceptional cases, both sets of results are reported. The total number of pyrethroid treatments for each site was calculated from Croft et al. (1989) by multiplying the total years of pyrethroid use by the average number of pyrethroid applications per season.

Statistical tests were done with SAS (SAS Institute 1985) unless noted otherwise.  $LC_{50}$  values were not normally distributed (Shapiro-Wilk test,  $W = 0.87$ ,  $P < 0.01$ ; SAS Institute 1985); logarithmic transformation yielded a normal distribution ( $W = 0.97$ ,  $P > 0.40$ ). All analyses were done on logarithmically transformed  $LC_{50}$ 's. Type III sums of squares were used for analysis of variance (ANOVA) and analysis of covariance (ANCOVA) (PROC GLM).

We used ANOVA to test for geographical variation in fenvalerate  $LC_{50}$ . Independent variables were region and subregion nested within region. Regression analysis (PROC REG) was used to test the relationship between fenvalerate  $LC_{50}$  at a given site and the number of pyrethroid treatments at that site. This association was tested for all sites pooled ( $n = 48$ ), for each region separately (four regions,  $n = 5$ –17 sites per region), and for each of the six subregions of Washington and Oregon ( $n = 4$ –6 sites per subregion). Separate regression tests were not done for the subregions of California because they had too few sites (Placerville subregion,  $n = 2$  sites) or no variation in number of treatments (Lake County subregion, all 3 sites had 20 treatments). The probabilities from each of the six independent subregion regressions were combined (Sokal & Rohlf 1969) to test the overall hypothesis that fenvalerate  $LC_{50}$  varied with number of pyrethroid treatments within subregions. Regression analysis was also used to test the association between fenvalerate  $LC_{50}$  at a given site and the mean number of pyrethroid treatments at other sites in the same subregion, called "neighboring treatments." The neighboring treatments variable was used as an index of subregional selection for pyrethroid resistance, whereas the site-specific reports of pyrethroid use measured local selection.

Residuals from the regression of number of pyrethroid treatments on fenvalerate  $LC_{50}$  were tested for effects of spray timing, continuity of pyrethroid use, and intensity of pear production (three-way ANOVA), and spatial effects (ANOVA with subregion nested within region).

We used ANCOVA to consider jointly the effects of number of treatments (covariate) and timing of treatments, continuity of treatments, intensity of pear reproduction, region, and subregion (class variables). An initial test showed homogeneity of slopes; none of the first order interactions between number of treatments and class variables (e.g., number of treatments  $\times$  timing of treatments) were significant. ANCOVA results reported are thus based on models with main effects only (interac-

**Table 1. Regional and subregional variation in fenvalerate LC<sub>50</sub> for pear psylla and number of pyrethroid treatments**

Area	No. sites	Mean LC <sub>50</sub> (range) (mg [AI]/liter)	Treatments $\bar{x}$ (range)
Regional			
British Columbia	10	33.9 (16.8–90.0)	10.4 (0–27)
Washington	16	87.1 (24.3–315)	12.7 (0–24)
Oregon	17	11.5 (2.1–64.5)	13.8 (0–22)
California	5	9.8 (3.6–19.8)	11.5 (0–20)
Subregional			
Washington			
N. Washington	4	41.7 (24.3–66.0)	8.8 (3–20)
Wenatchee	6	126 (49.5–282)	18 (0–24)
Yakima	6	95.5 (43.5–315)	10 (0–20)
Oregon			
Hood River	6	20.9 (9.9–64.5)	18.8 (11–22)
Willamette	6	11.2 (2.1–41.4)	7.3 (0–18)
Medford	5	5.9 (3.6–10.5)	15.2 (9–18)
California			
Lake Co.	3	19.1 (17.4–19.8)	20.0 (20)
Placerville	2	3.6 (3.6)	3.0 (0–5)

tions excluded). We used variance component analysis (PROC VARCOMP, Method = Type I) to estimate the relative influence of region and subregion on fenvalerate LC<sub>50</sub>.

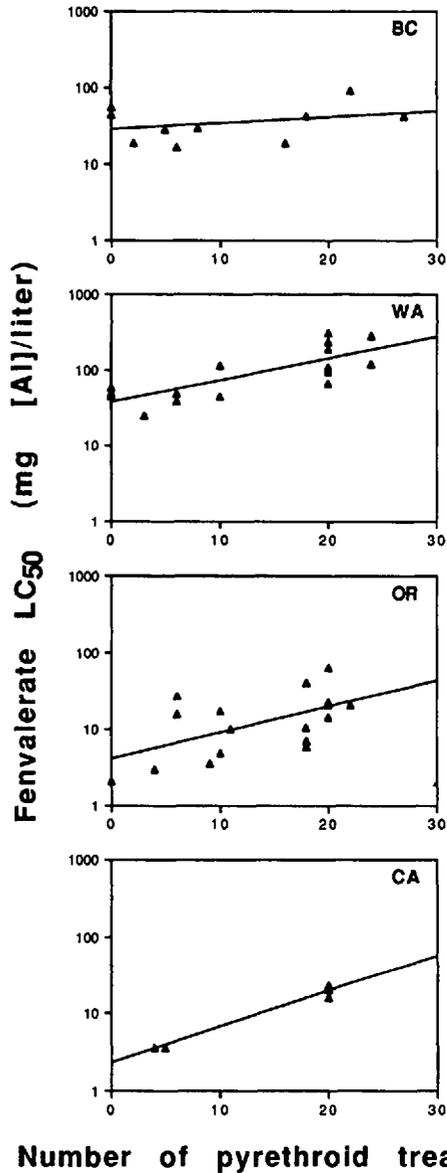
**Results**

**Geographical Variation in Fenvalerate Resistance.** Regional and subregional values for fenvalerate LC<sub>50</sub> of *P. pyricola* are given in Table 1. LC<sub>50</sub>'s varied significantly among regions and among subregions within regions (Table 2). The mean LC<sub>50</sub> for the state of Washington (87.1 mg [AI]/liter) was approximately 2.6, 7.6, and 8.9 times greater than the mean LC<sub>50</sub> of British Columbia, Oregon, and California, respectively. Maximum differences between subregional means within regions were 3-fold in Washington, 3.5-fold in Oregon, and 5.3-fold in California (Table 1).

**Fenvalerate LC<sub>50</sub> and Number of Pyrethroid Treatments.** The LC<sub>50</sub> generally increased across sites as the number of pyrethroid treatments increased (Fig. 1; Table 3). The regression between treatments per site and LC<sub>50</sub> at each site was significant overall ( $n = 48$ ,  $R^2 = 0.12$ ,  $P = 0.01$ ) and significant within three of the four regions (Washington, Oregon, and California; mean  $R^2 = 0.65 \pm 0.19$  SE) (Table 3). In the fourth region (British Columbia), however, the association between treatments and LC<sub>50</sub> was positive, but not significant ( $n = 10$ ,  $R^2 = 0.09$ ,  $P = 0.39$ ) (Table 3). For the three

**Table 2. ANOVA for regional and subregional variation in fenvalerate LC<sub>50</sub> in pear psylla**

Source	df	SS	MS	F	P
Region	3	7.26	2.42	5.95	0.042
Subregion (region)	5	2.03	0.41	4.54	0.002
Error	39	3.49	0.09	—	—



**Fig. 1.** Relationship between total number of pyrethroid treatments and fenvalerate LC<sub>50</sub> for pear psylla from British Columbia (BC), Washington (WA), Oregon (OR), and California (CA).

regions where the regression was significant, the estimated slopes were similar (Table 3), which suggests that the proportional increase in fenvalerate LC<sub>50</sub> per pyrethroid application was similar in each region. The intercept for Washington (95% CI = 23.4–58.9 mg [AI]/liter), however, was significantly greater than the intercepts for Oregon (95% CI = 1.56–10.2 mg [AI]/liter) or California (95% CI = 1.79–2.78 mg [AI]/liter), indicating that unsprayed sites in Washington would be expected to have a greater fenvalerate LC<sub>50</sub> compared with unsprayed sites in the other two states.

Within each of the three subregions of Wash-

**Table 3. Regression analysis of effect of number of pyrethroid sprays on logarithm of fenvalerate LC<sub>50</sub> within regions and within subregions**

Area	No. sites	Intercept ± SE	Slope ± SE	R <sup>2</sup>	P
All sites	48	1.16 ± 0.13	0.022 ± 0.009	0.12	0.01
Regional					
British Columbia	10	1.45 ± 0.11	0.007 ± 0.008	0.09	0.39
Washington	16	1.57 ± 0.09	0.029 ± 0.006	0.62	0.0003
Oregon	17	0.60 ± 0.19	0.034 ± 0.013	0.33	0.02
California	5	0.35 ± 0.03	0.046 ± 0.002	0.99	0.0002
Subregional					
Washington					
N. Washington	4	1.45 ± 0.09	0.020 ± 0.009	0.73	0.14
Wenatchee	6	1.69 ± 0.19	0.023 ± 0.010	0.58	0.08
Yakima	6	1.63 ± 0.13	0.034 ± 0.010	0.73	0.03
Oregon					
Hood River	6	0.61 ± 0.56	0.038 ± 0.029	0.30	0.26
Willamette	6	0.54 ± 0.23	0.069 ± 0.025	0.65	0.05
Medford	5	0.33 ± 0.19	0.030 ± 0.013	0.55	0.09

ington and the three subregions of Oregon, treatments and LC<sub>50</sub> were positively associated, but individual subregion regressions (four to six sites per subregion) were significant only for the Yakima and Willamette subregions (Table 3). The mean R<sup>2</sup> value for the regression between LC<sub>50</sub> and treatments per site within subregions was 0.59 (±0.07 SE, *n* = 6 subregions). An overall test that combined the probabilities from all six subregion regressions showed that fenvalerate LC<sub>50</sub> was significantly associated with number of treatments within subregions ( $-2 \sum \ln P = 29.5$ , *df* = 12, *P* < 0.005; Sokal & Rohlf 1969).

With all sites including the organic/low spray sites incorporated in the analysis, the mean LC<sub>50</sub> for each region was not correlated with the mean number of treatments per region (*R*<sup>2</sup> = 0.001, *P* = 0.89, *n* = 4 regions), nor was the mean LC<sub>50</sub> for each subregion correlated with the mean number of treatments per subregion (*R*<sup>2</sup> = 0.11, *P* = 0.38, *n* = 9 subregions). With the organic/low spray sites excluded, these associations were much stronger but not significant (regional: *R*<sup>2</sup> = 0.46, *P* = 0.32, *n* = 4; subregional: *R*<sup>2</sup> = 0.28, *P* = 0.15, *n* = 9).

Results showed no significant association between the fenvalerate LC<sub>50</sub> at a particular site and the mean number of pyrethroid treatments at the other sites in the same subregion (called "neighboring treatments"). Simple linear regression showed an insignificant positive association between neighboring treatments and LC<sub>50</sub> over all sites (*R*<sup>2</sup> = 0.009, *P* = 0.53, *n* = 48). Multiple linear regression, which included number of treatments per site and thus removed the effect of the positive correlation between number of treatments per site and neighboring treatments (*r* = 0.39, *P* = 0.005, *n* = 48), again showed an insignificant association between neighboring treatments and LC<sub>50</sub> (slope ± SE = -0.0036 ± 0.015, *P* = 0.82, *n* = 48). In addition, multiple linear regression showed no significant association between neighboring treatments and LC<sub>50</sub> within Washington, Oregon, or

California. Because British Columbia had only one subregion, it could not be tested separately in this analysis.

In summary, variation in total number of pyrethroid treatments accounted for a significant portion of the variation in fenvalerate LC<sub>50</sub> over all sites (*R*<sup>2</sup> = 0.12), within three of four regions (mean *R*<sup>2</sup> = 0.65 ± 0.19 SE, *n* = 3 states), and within subregions (mean *R*<sup>2</sup> = 0.59 ± 0.07 SE, *n* = 6 subregions). However, variation in number of treatments was not significantly associated with fenvalerate LC<sub>50</sub> within the fourth region, British Columbia. The trends with organic/low spray sites excluded suggest that variation in number of treatments may explain some of the variation in LC<sub>50</sub> across regions and across subregions. The number of treatments at neighboring sites within a subregion was not significantly associated with LC<sub>50</sub> at a given site over the entire sample or within states.

**Fenvalerate LC<sub>50</sub> and Timing of Treatments, Continuity of Treatments, and Intensity of Surrounding Pear Production.** The timing of treatments, continuity of treatments, and intensity of surrounding pear production were significantly associated with the total number of treatments per site (ANOVA, *P* < 0.003 for each effect). Sites that were treated both during prebloom and summer, sites where annual pyrethroid use was continuous, and sites surrounded by high intensity of pear production generally had more total pyrethroid treatments than did other sites. Thus, to test for direct effects of timing, continuity, and intensity on LC<sub>50</sub>, we examined their influence on the residuals from the regression of number of treatments on LC<sub>50</sub>.

Over all sites, timing of treatments, continuity of treatments, and intensity of surrounding pear production had no significant effect on the regression residuals (ANOVA, *P* > 0.40 for each effect). Timing, continuity, and intensity also had no significant effect on the residual variation from the within-region regressions (ANOVA, *P* > 0.05 for each effect within regions).

**Table 4.** ANCOVA for effects of timing of treatments, continuity of treatments, intensity of surrounding pear production, number of treatments, region, and subregion on fenvalerate LC<sub>50</sub>

Source	df	SS	MS	F	P
Timing of treatments	3	0.10	0.03	0.52	0.67
Continuity of treatments	1	0.003	0.003	0.04	0.84
Intensity of pear production	2	0.05	0.03	0.39	0.68
Number of treatments	1	0.32	0.32	4.87	0.03
Region	3	5.63	1.88	10.76	0.01
Subregion (region)	5	0.87	0.17	2.68	0.04
Error	32	2.08	0.07	—	—

**Empirical Model of Variation in Fenvalerate Resistance.** Results of ANCOVA showed that number of pyrethroid treatments, region, and subregion had a significant effect on fenvalerate resistance whereas timing of treatments, continuity of treatments, and intensity of pear production in the surrounding area did not (Table 4). The ANCOVA model based on all six of the aforementioned independent variables explained 84% of the variation in fenvalerate LC<sub>50</sub> across all sites. An ANCOVA model based only on the three significant independent variables (number of treatments, region, and subregion) explained 83% of the variation in fenvalerate LC<sub>50</sub> across all sites ( $F = 19.9$ ,  $df = 9, 38$ ;  $P < 10^{-6}$ ).

Both region and subregion explained a significant portion of the residual variation from the regression of number of treatments on LC<sub>50</sub> (Table 5), which shows that for a given number of pyrethroid treatments, the expected fenvalerate LC<sub>50</sub> varied significantly among regions and subregions. As previously noted, variation in number of treatments explained 12% of the variation in fenvalerate resistance across all sites (Table 3). Of the 88% residual variation from the regression of number of treatments on fenvalerate resistance, region accounted for 69% and subregion accounted for 12%. Estimated contributions to overall variation in fenvalerate LC<sub>50</sub> were thus: treatments = 12%, region = 61% ( $69\% \times 0.88$  residual), and subregion = 10% ( $12\% \times 0.88$  residual).

### Discussion

Our analysis showed significant variation in fenvalerate resistance among regions and subregions. Previously reported pairwise comparisons showed significant differences in fenvalerate resistance between orchards within all subregions except Medford, Ore., Lake County, Calif., and Placerville, Calif. (Croft et al. 1989). This pattern of regional, subregional, and local variation suggests that factors influence resistance development at each of these spatial scales.

Analysis of electrophoretic variation at eight polymorphic loci in 18 populations of pear psylla from British Columbia, Washington, Oregon, and California shows that allozyme variation within regions was equal to or greater than variation be-

**Table 5.** ANOVA for effects of region and subregion on residuals from regression of number of pyrethroid treatments on fenvalerate LC<sub>50</sub> in pear psylla

Source	df	SS	MS	F	P
Region	3	7.76	2.59	11.15	0.012
Subregion (region)	5	1.16	0.23	3.98	0.005
Error	39	2.27	0.06	—	—

tween regions (Unruh in press). These results imply that regional patterns of insecticide resistance in pear psylla are best explained by differences in regional selection pressures rather than genetic drift between populations of different regions (Unruh in press).

A plausible hypothesis is that regional and subregional differences in pyrethroid use caused regional and subregional differences in fenvalerate resistance. We cannot strongly refute or confirm this hypothesis because analysis with all sites included suggests no association between mean number of pyrethroid treatments and mean fenvalerate LC<sub>50</sub> across regions and subregions, whereas the trend with organic/low spray sites excluded suggests that regional and subregional differences in pyrethroid use may explain some of the variation in fenvalerate resistance among regions and subregions. A more extensive survey of pyrethroid use in each region could clarify this issue. Nonetheless, regional and subregional differences explained a significant portion of the residual variation from the regression of number of treatments on fenvalerate LC<sub>50</sub>, indicating that variation in LC<sub>50</sub>'s among regions and subregions was not entirely explained by variation in number of treatments.

Other factors that might account for regional and subregional differentiation can be grouped into two categories: environmental and genetic. Because pear psylla were sampled from the field, environmental differences between regions and subregions may have contributed to variation in susceptibility. Environmental factors that may differ among regions and subregions that could have affected mortality in bioassays include climate, pear cultivar, plant condition (e.g., water and nutritional status), and cultural practices. Environmental factors also include any differences between regions in bioassays. Efforts were made to conduct bioassays uniformly across regions, but the tests were done in several different laboratories, so systematic differences in procedure cannot be ruled out. Genetic differences in susceptibility between regions could be caused by cross-resistance from previously used insecticides (Croft et al. 1989); regional patterns of fenvalerate resistance were similar to regional resistance patterns for organophosphorous insecticides (Riedl et al. 1981). Regional patterns may also reflect historical, stochastic events such as the occurrence of key mutations. Resistance has generally been most serious in Washington, the first western state colonized by pear psylla (Westgard & Zwick 1972, Follett et al. 1985, Croft et al. 1989).

Bioassays of pear psylla from different regions reared and tested in a common environment are needed to distinguish between genetic and environmental influences on resistance.

With the exception of British Columbia, which is discussed below, much of the variation in fenvalerate  $LC_{50}$  within regions and subregions was attributable to variation in number of pyrethroid treatments. In particular, fenvalerate resistance across sites increased as the number of pyrethroid treatments increased. Treatments at neighboring sites, timing of treatments, continuity of treatments, and intensity of pear production in the surrounding area showed no significant effect on  $LC_{50}$  of fenvalerate in our analysis.

Results showing that fenvalerate  $LC_{50}$  of pear psylla was more strongly associated with the treatment history of individual orchards than with subregional treatment history contrast with the roughly equal influence of in-orchard and county-wide treatments on resistance development in *Aphytis melinus* in California (Rosenheim & Hoy 1986). Our index of subregional treatment history for pear psylla, however, was based on relatively few sites per subregion and inaccuracy in this index might have obscured a significant relationship between it and fenvalerate resistance. Nonetheless, for Washington, California, and Oregon, local pyrethroid use explained, on average, more than half of the local variation in fenvalerate susceptibility, whereas subregional treatment history had no detectable effect. These results suggest that populations responded much more strongly to local selection than to subregional selection. Results from the diamondback moth, *Plutella xylostella* (L.), in Hawaii also suggest strong effects of local selection (Tabashnik et al. 1987).

Significant local variation in fenvalerate resistance in pear psylla may seem paradoxical because populations are thought to disperse widely during fall migrations (Follett et al. 1985). Recent population genetic studies based on allozymic variation suggest, however, that gene flow among populations is low compared with the intensity of selection for resistance (Unruh in press). Our results showing that orchard treatment history explains much of the local variation in fenvalerate resistance support the hypothesis that gene flow is too weak to substantially alter the response to selection.

Fenvalerate resistance generally increased with number of pyrethroid sprays, but this association was not significant in British Columbia. In all regions except British Columbia, most pyrethroid treatments were fenvalerate. In British Columbia, however, permethrin was the most commonly used pyrethroid, with more recent additions of deltamethrin and cypermethrin (Croft et al. 1989). Thus, for Washington, Oregon, and California, the number of pyrethroid treatments is a good indicator of fenvalerate use; for British Columbia it is not. Therefore, it is not surprising that the  $LC_{50}$  for fenvalerate was more closely associated with num-

ber of pyrethroid treatments in the western United States than in British Columbia. The weak positive association between fenvalerate  $LC_{50}$  and pyrethroid treatments suggests that permethrin selects only weakly for cross-resistance to fenvalerate. We cannot exclude the possibility, however, that other factors (e.g., more movement between sites) decrease the association between local pyrethroid treatment history and fenvalerate susceptibility in British Columbia.

Previous studies noted an especially strong association between treatment history and resistance levels in the Willamette Valley, Oregon, for azinphosmethyl, endosulfan (Follett et al. 1985), and fenvalerate (Croft et al. 1989). Our analysis showed that Willamette was one of the two subregions where the regression between fenvalerate  $LC_{50}$  and number of pyrethroid treatments was significant at  $P = 0.05$  (Table 3). The slope of the regression for Willamette (0.069) was more than double the mean slope of the other five subregion regressions (0.029), but was not significantly greater than the others because of relatively large errors of estimation (Table 3). More intensive sampling within subregions would provide a better test of the hypothesis that the slope in Willamette is greater than in other subregions.

Results from our analysis have both discouraging and encouraging implications for managing insecticide resistance in pear psylla. If regional differences in fenvalerate resistance were caused by previous use of other insecticides or other historical factors, then the prospects for regional management of pyrethroid resistance are not bright. In addition, many of the pear psylla populations in Washington, particularly in the Wenatchee and Yakima subregions, had an  $LC_{50} > 80$  mg (AI)/liter; this level of resistance is likely to be high enough to cause field control failure (Croft et al. 1989). Although only one population in British Columbia had an  $LC_{50} > 80$  mg (AI)/liter, many populations from that province had substantial resistance (Table 1). Where high levels of resistance already exist, resistance management options are limited.

No population outside of Washington and British Columbia had an  $LC_{50} > 80$  mg (AI)/liter. Therefore, managing pyrethroid resistance may be possible in Oregon and California. Further, a significant portion of variation in susceptibility within states and within subregions was attributable to variation in number of pyrethroid treatments per orchard. Thus, some local management of pyrethroid resistance in pear psylla is possible. A grower who reduces the number of treatments can expect to reduce the rate of resistance development in his or her orchard, even if the orchard is in an area where other growers treat frequently and resistance is generally high.

Retrospective analyses of patterns of insecticide resistance such as ours have certain limitations including lack of true controls and difficulty in ensuring that the field sites selected represent an un-

biased sample. Even so, such analyses have advantages compared with experimental studies of resistance. Retrospective studies can incorporate long time periods and large numbers of commercial sites over wide areas, thus providing information about resistance evolution under field conditions of practical importance. We encourage researchers to extend analysis of bioassay data beyond pairwise comparisons of populations to include consideration of the spatial scale and causes of variation in pesticide resistance.

#### Acknowledgment

We are grateful to M. Caprio, F. Gould, P. S. Leung, T. Unruh and the pear psylla working group for their thoughtful suggestions. Special thanks go to T. Unruh for providing a preprint of his paper and to N. Finson and S. Toba for technical assistance. This work was supported by USDA grants HAW00947H, Western Regional IPM grant 8902553, USDA/CSRS Special Grants in Tropical and Subtropical Agriculture 8902558, and a Fujio Matsuda Scholar award from the University of Hawaii Foundation. This is paper no. 3365 of the Hawaii Institute of Tropical Agriculture and Human Resources Journal series.

#### References Cited

- Croft, B. A., E. C. Burts, H. E. van de Baan, P. H. Westigard & H. Riedl. 1989. Local and regional resistance to fenvalerate in *Psylla pyricola* Foerster (Homoptera: Psyllidae) in western North America. *Can. Entomol.* 121: 121-129.
- Follett, P. A., B. A. Croft & P. H. Westigard. 1985. Regional resistance to insecticides in *Psylla pyricola* from pear orchards in Oregon. *Can. Entomol.* 117: 565-573.
- Georghiou, G. P. 1986. The magnitude of the resistance problem, pp. 14-43. In National Research Council, Pesticide resistance: strategies and tactics for management. National Academy of Sciences, Washington, D.C.
- Miranowski, J. A. & G. A. Carlson. 1986. Economic issues in public and private approaches to preserving pest susceptibility, pp. 436-448. In National Research Council, Pesticide resistance: strategies and tactics for management. National Academy of Sciences, Washington, D.C.
- National Research Council. 1986. Pesticide resistance: strategies and tactics for management. National Academy of Sciences, Washington, D.C.
- Riedl, H., P. H. Westigard, R. S. Bethell & J. E. DeTar. 1981. Problems with chemical control of pear psylla. *Calif. Agric.* 35(9-10): 7-9.
- Rosenheim, J. A. & M. A. Hoy. 1986. Intraspecific variation in levels of pesticide resistance in field populations of a parasitoid, *Aphytis melinus* (Hymenoptera: Aphelinidae): the role of past selection pressures. *J. Econ. Entomol.* 79: 1161-1173.
- Roush, R. T. & B. E. Tabashnik [eds.]. In press. Pesticide resistance in arthropods. Chapman & Hall, New York.
- SAS Institute. 1985. SAS user's guide: statistics, version 5 ed. SAS Institute, Cary, N.C.
- Sokal, R. R. & F. J. Rohlf. 1969. Biometry. Freeman, San Francisco.
- Tabashnik, B. E. 1986. Computer simulation as a tool for pesticide resistance management, pp. 194-206. In National Research Council, Pesticide resistance: strategies and tactics for management. National Academy of Sciences, Washington, D.C.
- Tabashnik, B. E., N. L. Cushing & M. W. Johnson. 1987. Diamondback moth (Lepidoptera: Plutellidae) resistance to insecticides in Hawaii: intra-island variation and cross-resistance. *J. Econ. Entomol.* 80: 1091-1099.
- Taylor, C. E. 1983. Evolution of resistance to insecticides: the role of mathematical models and computer simulations, pp. 163-173. In G. P. Georghiou & T. Saito [eds.], Pest resistance to pesticides. Plenum, New York.
- Unruh, T. H. In press. Genetic structure among 18 West Coast pear psylla populations: implications for the evolution of resistance. *Bull. Entomol. Soc. Am.*
- Van de Baan, H., P. H. Westigard, E. C. Burts & B. A. Croft. 1989. Seasonal susceptibility to insecticides in insecticide resistant pear psylla, *Psylla pyricola* (Homoptera: Psyllidae). *Crop Prot.* 8: 122-126.
- Westigard, P. H. & R. W. Zwick. 1972. The pear psylla in Oregon. *Oregon State Agricultural Bulletin* 122, Corvallis.

Received for publication 1 August 1989; accepted 12 October 1989.